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Mass loss, nutrient dynamics and influence of Diptera larvae in decomposing litter of *Erica tetralix* and *Molinia caerulea*

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With 4 figures

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1. Introduction

Wet heathlands in Western Europe were originally dominated by *Erica tetralix* L. (cross leaved heather). During the last few years on a large number of sites the plant communities that were dominated by *Erica tetralix* have been replaced by monocultures of *Molinia caerulea* (L.) MOENCH[1] (purple moor grass). It has been shown (BERENDSE & AERTS 1984) that this increase in *Molinia caerulea* may have been caused by an increased availability of nutrients.

In nutrient-poor ecosystems litter production and decomposition strongly regulate the availability of nutrients for uptake by plants (ROSSWALL & GRANHALL 1980) and thereby influence the relative abundance of the different plant species (PERSSON 1980). The rate of decomposition is influenced by a number of factors including moisture, temperature and soil acidity. Several studies have pointed to the fact that the soil fauna has an important effect on the rate of decomposition and nutrient release (ANDERSON *et al.* 1982; BERG *et al.* 1980b; EDWARDS 1974; SWIFT *et al.* 1979).

Substrate quality, as defined by the chemical composition of the decomposing material, has been considered to be a critical factor as well in determining the rate of decay. Chemical indices of substrate quality include element concentrations and concentrations of various classes of organic compounds. Nitrogen, phosphorus and lignin are considered to be important factors governing the rate of decomposition and nutrient release. The litter decomposition rate is positively correlated with the concentration of nitrogen and phosphorus, and negatively correlated with the lignin level in the decomposing material (BERG & STAAF 1980; MELILLO *et al.* 1982). In addition, mineralization of nitrogen and phosphorus occurs when, respectively, the C/N-ratio and the C/P-ratio has reached a level at which the nitrogen and phosphorus availability is no longer limiting to the organisms decomposing the litter (SWIFT *et al.* 1979; BERG & STAAF 1981).

Previous studies have shown that both the nitrogen and the phosphorus concentration of fresh *Molinia* litter are lower than those in fresh *Erica* litter. Thus, a higher mass loss rate is expected in the *Erica* litter. *Erica* litter consists of leaves, flowers and stems; the nitrogen and phosphorus concentration of stems has found to be lower than that of leaves and flowers. The presence of *Erica* stems is expected to decrease the decomposition rate of the *Erica* litter.

In this paper the effects of the chemical composition on the rate of decomposition and the rate of nutrient release are considered. In addition, we consider the effects of observed soil fauna activity.

2. Material and methods

The litter was collected in late September by cutting dead leaves and dead culms from *Molinia* and dead stems from *Erica*. The dead flowers and leaves of *Erica* were collected by shaking the *Erica* plants.

[1]) Nomenclature according to H. HEUKELS & S. J. VAN OOSTSTROOM, Flora van Nederland.

Table 1. The composition of the litter used in the three categories given as a percentage of the dry mass at the start of the experiment

	Erica T	*Erica* L		*Molinia*
stems	10	2	leaves	99
leaves	55	65	culms	1
flowers	34	31		
organic remainder	1	2		

The leaf litter was divided into three categories: *Molinia litter* (M), *Erica* leaf and flower litter (EL) and *Erica* leaf, flower and stem litter (ET). The composition of these categories is mentioned in Table 1.

The litter was reduced to a maximum length of about 2 cm and air-dried for two days at room temperature. After this period the variability in the moisture level was very low (s.d. = 1.5%).

For each category 90 petri dishes were filled with about 2 g litter (dry mass) and were stored in a room with constant climatic conditions (22 °C and R. H. 80%). The litter was aerated by three small holes in the lid of the petri dishes. The moisture level was kept constant at about 80 to 88% by the regular addition of demineralized water. The total duration of the experiment was 52 weeks. The litter in various categories was sampled on 9 dates at intervals varying from 2 weeks at the beginning of the experiment to 14 weeks at the end. On each date the dry mass of the litter in 10 petri dishes of each category was determined after it had been dried for 48 h at 70 °C. Inorganic nitrogen and phosphorus contents were determined by extraction, namely by shaking about 1 g fresh litter in 100 ml H_2O at 120 rpm for 120 min. For the determination of total nitrogen and phosphorus, the remaining litter was dried (70 °C for 48 h), ground, and digested in H_2SO_4 and H_2O_2. Concentrations of ammonium and phosphate were determined colorimetrically by means of an autoanalyzer. The differences between total and inorganic nitrogen and phosphorus were considered to be the amount of organic nitrogen and phosphorus.

The lignin content of the litter was determined by extraction with sulphuric acid. These extractions were carried out under supervision of Dr. B. BERG at the Department of Ecology and Environmental Research of the Swedish University of Agricultural Sciences, Uppsala, Sweden (method described by BERG *et al.* 1980a).

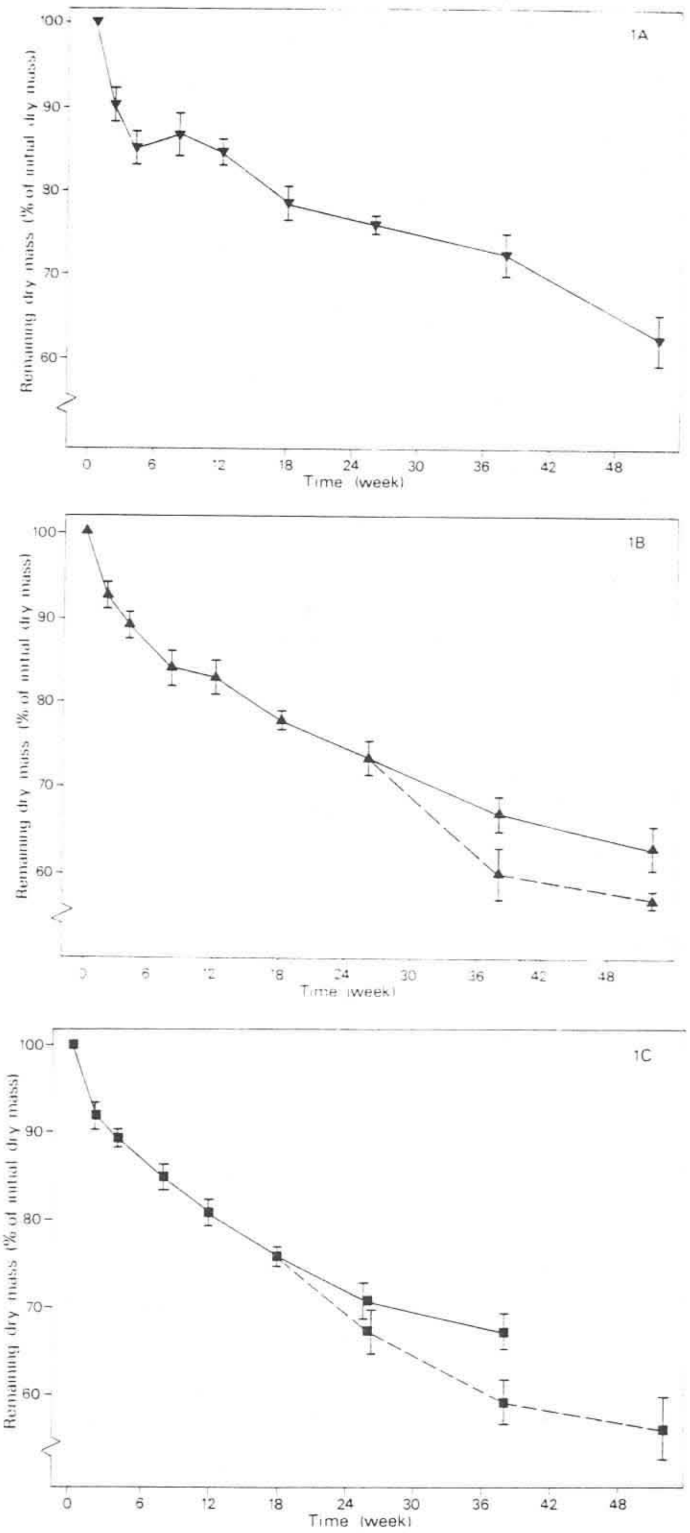
After 18 weeks we found that approximately half the samples of ET and EL contained larval and adult Diptera. The presence of the Diptera seemed to occur at random: no other differences between these samples and the samples without Diptera were observed. Since at the end of the experiment all the Diptera had died, we were not able to determine the species. The larvae had an important comminuting effect on the litter. The remaining leaf litter in these samples was amorphous and no individual elements could be recognized any longer. The samples with the Diptera were seperated by eye on the presence of the larvae and/or adult Diptera after 26 and 38 weeks, and on the presence of the empty larval skins after 52 weeks. On the last sampling date there were no samples left of EL without Diptera.

The dry mass and the nitrogen and phosphorus content of the total litter including the Diptera were determined in each individual sample. A pairwise comparison of all results was carried out, using the Student t-test. When samples with and without Diptera were separated, each sampling consisted of 3 up to 10 replicates. In the case of two samplings (at 0 weeks for ET and EL, and at 18 weeks for ET, EL and M) there was reason to assume that the analyses of total nitrogen and phosphorus were not correct. Because of the lack of material the analyses could not be repeated for each individual sample. Therefore, in these cases duplicate analyses were performed in a bulked sample.

3. Results

In the *Erica* litter higher concentrations of nitrogen and phosphorus were found compared to the *Molinia* litter (Table 2). Furthermore, the lignin concentration in the *Erica* litter was about twice as high as that in the *Molinia* litter. No differences in initial litter quality were found between the two *Erica* litter types.

Fig. 1. Remaining dry mass of the three litter types vs. time. The dashed lines indicate the remaining dry mass in the litter samples with Diptera larvae present.
A) (▼—▼) *Molinia* litter;
B) (▲—▲) *Erica* T (leaves, flowers and stems) litter;
C) (■—■) *Erica* L (laeves and flowers) litter.
The standard errors are indicated by vertical bars.


1A
1B
1C
Remaining dry mass (% of initial dry mass)
100
90
80
70
60
0
6
12
18
24
30
36
42
48
Time (week)

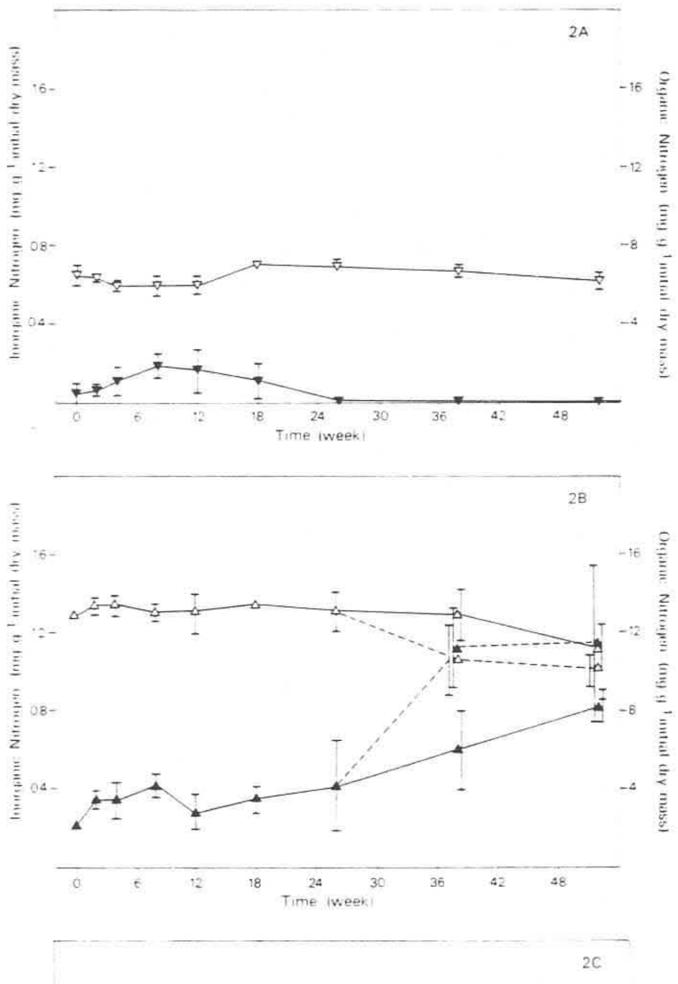


Fig. 2. The amounts of organic (blank symbols) and inorganic (closed symbols) nitrogen in the three litter types vs time. The dashed lines indicate the changes in the litter samples with Diptera larvae present.

A) (▼—▼) *Molinia* litter;
B) (▲—▲) *Erica* T litter;
C) (■—■) *Erica* L litter.

The standard errors are indicated by vertical bars.

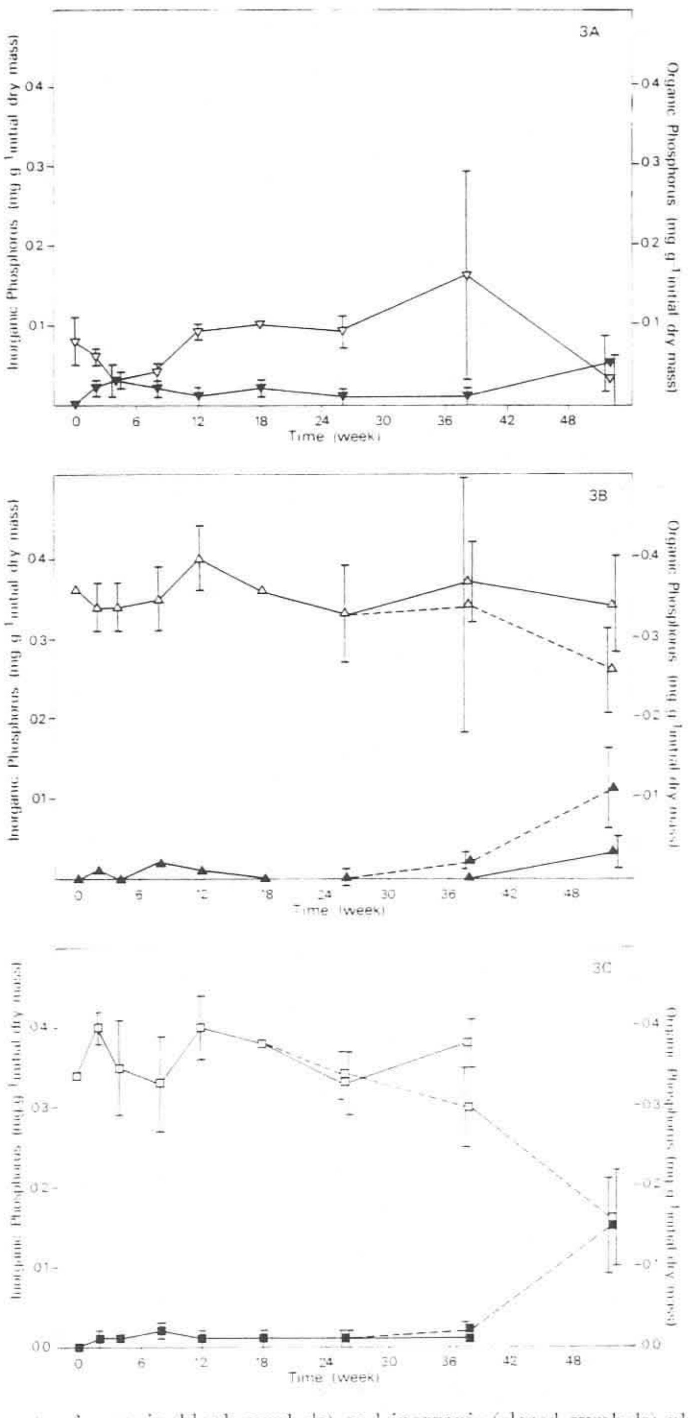


Fig. 3. The amounts of organic (blank symbols) and inorganic (closed symbols) phosphorus in the three litter types vs. time. The dashed lines indicate the changes in the litter samples with Diptera larvae present.

A) (▼—▼) *Molinia* litter;
B) (▲—▲) *Erica* T litter;
C) (■—■) *Erica* L litter.

The standard errors are indicated by vertical bars.

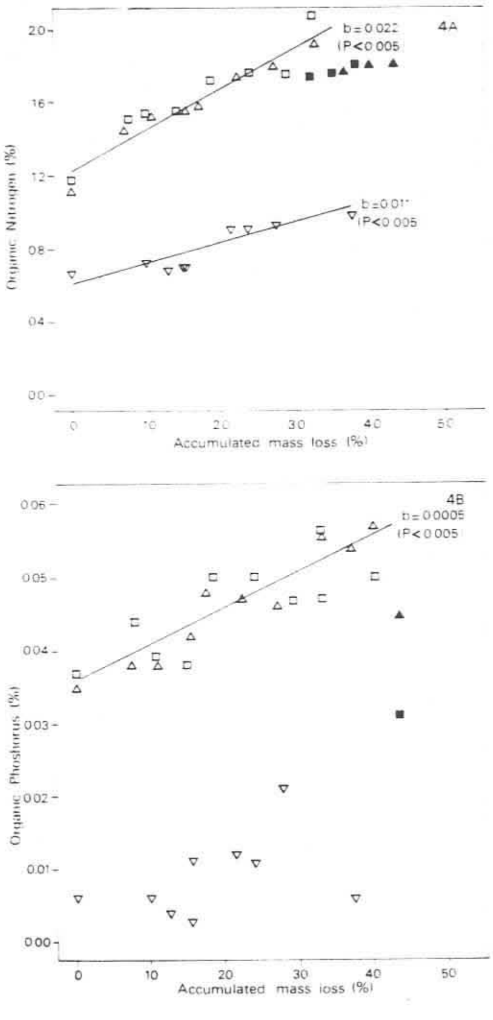


Fig. 4. The relationship between the concentration of organic nitrogen (A) and phosphorus (B) and the accumulated mass loss. *Molinia* litter (▽—▽): *Erica* T litter (△—△): *Erica* L litter (□—□). The closed symbols indicate mineralization.

Table 2. The initial litter quality of the three litter categories in mg per g dry mass

	Erica T	*Erica* L	*Molinia*
inorganic nitrogen	.24	.22	.05
organic nitrogen	11.6	11.2	6.5
inorganic phosphorus	.00	.00	.00
organic phosphorus	.37	.35	.06
lignin	463	444	237

After 52 weeks the three different categories of litter had lost about 35% of their initial dry mass, with no significant differences between them. However, the *Molinia* litter showed a significantly higher mass loss ($p < 0.01$) during the first 4 weeks. The mass loss of the *Erica* litter (ET and EL) was significantly higher ($p < 0.01$) in the samples with observed larval activity than in those without the larvae present (Fig. 1).

During the first half of the experiment the amount of inorganic nitrogen increased and decreased again ($p < 0.01$) in all three litter types (Fig. 2). In the *Molinia* litter no inorganic nitrogen was found during the second half of the experiment. In the *Erica* T litter the amount of inorganic nitrogen increased significantly ($p < 0.01$) during this period. The activity of the Diptera larvae resulted in a significantly ($p < 0.01$) higher amount of inorganic nitrogen in the *Erica* litter. Up to 38 weeks after the start of the experiment the amount of inorganic phosphorus in the three litter types remained at a nearly constant level (Fig. 3). After that date all litter types showed a significant ($p < 0.01$) increase in the amount of inorganic phosphorus. In the *Erica* T litter this amount was significantly ($p < 0.01$) higher when larvae were present. In general, the dynamics of organic nitrogen and phosphorus showed a pattern opposite to that of the dynamics of inorganic nitrogen and phosphorus.

In litter of both species, a linear relation was found between the percentage organic nitrogen and the accumulated percentage mass loss ($p < 0.005$), as long as no mineralization occured (Fig. 4). Mineralization in the *Erica* litter coincided with a decrease in the slope of this relation. In the *Erica* litter a linear relation between the percentage organic phosphorus and the accumulated percentage mass loss was found ($p < 0.005$). In the *Molinia* litter there was no significant linear correlation between percentage organic phosphorus and accumulated percentage mass loss.

4. Conclusions and discussion

Berg & Staaf (1980) distinguish an early nutrient-regulated phase and a later lignin-regulated phase within the decomposition process. During this early period a higher nitrogen and phosphorus concentration leads to a higher decomposition rate. The higher mass loss that we expected in the *Erica* litter, on the basis of the higher initial nitrogen and phosphorus level did not occur in this experiment. On the contrary, *Molinia* showed a higher mass loss during the first 4 weeks of the experiment. This cannot be explained by the difference in initial nitrogen and phosphorus level. Decomposition experiments with *Erica* and *Molinia* litter, carried out under field conditions, have shown a higher mass loss in *Molinia* litter than in *Erica* litter (Berendse & Rouwenhorst, unpublished results).

In our experiment, performed under controlled laboratory conditions, the input of nutrients from the environment was excluded. Thus, microorganisms and soil fauna involved in litter decomposition had to rely completely on the original nitrogen and phosphorus stocks of the death plant tissues. So, a clear negative effect of the low nitrogen and phosphorus concentration in the decomposition of *Molinia* litter would be expected in this experiment.

Several authors have pointed to the retarding effect that a high initial lignin level has on the decomposition rate (Fogel & Cromack 1977; Berg & Staaf 1980). The initial lignin concentration in the *Erica* litter is found to be two times as high as the initial lignin concentration in the *Molinia* litter. So, the retarding effect of lignin is expected to be stronger in the *Erica* litter than in the *Molinia* litter. *Melillo et al.* (1982) have pointed to the important role of the ratio "initial lignin content: initial nitrogen content" in determining the decomposition rate. In our experiment the ratio was found to be 37 to 38 for both the *Erica* and the *Molinia* litter. So, on the basis of this ratio no differences in mass loss between *Erica* and *Molinia* litter would be expected.

In all categories the amount of inorganic nitrogen increased during the first 8 weeks of the experiment. This increase may be due to leaching (Berg & Staaf 1981). Afterwards, the inorganic nitrogen is immobilized again. In *Molinia* litter and *Erica* L. litter no further mineralization is found; in *Erica* T litter a slight mineralization of nitrogen (mainly ammonium) at the end of the experiment is noticed. By this time the C/N-ratio of the *Erica* litter had decreased to 25—28 (estimating the carbon content at 50%). It is at this level that the critical nitrogen level is though to be reached (Staaf & Berg 1982). Although increases and decreases in organic nitrogen seem to correspond, they were not found to compensate each other quantitatively. These differences may have been caused by the loss of volatile nitrogen compounds.

Mineralization of phosphorus in *Erica* litter started during the interval between the samplings at 38 and 52 weeks. By this time the C/P-ratio had decreased to approximately 900. The phosphorus concentrations found in *Molinia* litter suggest that mineralization occurred during the first 4 weeks and at the end of the experiment. At that time the C/P-ratio had decreased to approximately 5.000. The analysing technique and the low phosphorus concentrations in the *Molinia* litter are believed to have caused the considerable variation in these results.

Aber & Melillo (1980) conclude from a literature survey that, in general, there is a linear relationship between the percentage litter remaining and the nitrogen concentration in the residual material. As an important condition they mention the availability of a continuous external source of nitrogen. Although the input of nutrients in our experiment was excluded, here also a linear relationship was found during the immobilization phase. This linear relation is not surprising: a mass loss of 50% will lead to a doubled nitrogen concentration. Mineralization, which occurred in the ET litter and in the ET and EL litter with larvae, changed this relation. Not all the nitrogen is retained in the residual material, causing a decrease in the slope.

The Diptera larvae increased mass loss and the mineralization of nitrogen and phosphorus. This increased mineralization is shown both by the decrease in the organic and the increase in the inorganic nitrogen and phosphorus content. Soil fauna may influence decomposition in various ways, either directly by consumption of litter or indirectly by affecting the micro-organisms involved in the decomposition of various components (Swift *et al.* 1979; Berg *et al.* 1980b; Anderson *et al.* 1981). Direct 'mechanical' eating by animals causes a higher mass loss in litter because animals open up substrates, which leads to higher accessibility to microorganisms. Edwards (1974) concludes that Diptera larvae are extremely common in leaf litter and decaying wood. The majority of these species are saprophagous and have a significant contribution to litter breakdown. The increase of mass loss in our experiment can probably be attributed to an increased respiration caused by the activity of the Diptera larvae. Anderson *et al.* (1981) conclude that a common characteristic of soil fauna is that they excrete nitrogen-rich substances. This could be an important cause of the increased mineralization of nitrogen such as we have found in our experiment.

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An experiment was carried out to study the decomposition of litter of *Erica tetralix* and *Molinia caerulea* under controlled conditions. The input of nutrients during the experiment was excluded. The two litter types were different in nitrogen, phosphorus, and lignin concentration.

After 52 weeks of incubation no differences were found in mass loss between the litter of the two species. In the litter of *Molinia caerulea* the low nitrogen and phosphorus content had a retarding effect on mineralization of nitrogen and phosphorus. In the litter of *Erica tetralix* mineralization of nitrogen and phosphorus occurred when the C/N-ratio and the C/P-ratio had decreased to approximately 26 and 900 respectively. Diptera larvae were found to increase mass loss and to have a positive effect on mineralization of nitrogen and phosphorus in the litter of *Erica tetralix*.

Key words: decomposition, nitrogen, phosphorus, lignin, Diptera larvae, *Erica tetralix*, *Molinia caerulea*.